Year 1 Final report 22nd August 2013

Re-engineering the stomatopod eye, nature's most comprehensive visual sensor

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Justin Marshall
Sensory Neurobiology Group
Queensland Brain Institute
University of Queensland
St Lucia
Brisbane
Queensland 4072
AUSTRALIA

Contact Information and websites:

Ph - +61 (0)7 33651397
Fax - +61 (0)7 33654522
Cell - 0423 024162

Marshall lab Website:
www.uq.edu.au/ecovis
CoralWatch website:
www.coralwatch.org

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Justin Marshall

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14. ABSTRACT
In this final report, we show behavioural tests of colour and polarisation show coarse discrimination in stomatopods, which could be a new form of visual processing. Additionally, this is the first real time underwater linear polarisation camera built and tested in field. The report also discuss that [olarisation properties of reef animals, reflections, camouflage and light field baseline data begun. Photonic properties of silvery guanine crystals in fish skin determined and published in Nature journals. This is the first fluorescent staining of stomatopod eye and brain neuroarchitecture, and we discuss the ultrastructure of polarisation signal mechanism in stomatopods modelled.

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Introductory Remarks

Although this is being presented as a Final Report, it is important to emphasise that this is a four year on-going research collaboration for which this report details the first years achievements under grant number 12-1-4063.

Also notable is the intensely collaborative nature of what we are attempting and after the first year the team has worked well together on several of the sub projects and made plans for directions and work in the remaining 3 years. As a result, the publications and projects completed, as detailed below, are not just the output of the Marshall laboratory and are contributed to by Cronin, Roberts and Gruev as well as our respective postgrads and PhD students.

The productivity of our combined efforts are also greatly enhanced by being able to build on previously funded AOARD and AFOSR grants and contracts.

The original objectives of this collaborative four year project are detailed below with details of the outputs this year. Those components that are expected to be covered / achieved in the 2014 year are coloured red.

Year 1 achievements summary

•Behavioural tests of colour and polarisation show coarse discrimination in stomatopods. New form of visual processing implicated?

•First real time underwater linear polarisation camera built and tested in field.

•Polarisation properties of reef animals, reflections, camouflage and light field baseline data begun.

•Photonic properties of silvery guanine crystals in fish skin determined and published in Nature journals. Application in LED / light guides?

•First fluorescent staining of stomatopod eye and brain neuroarchitecture.

•Ultrastructure of polarisation signal mechanism in stomatopods modelled

(1) To learn the design foundations stomatopods use for optimized, rapid processing of multi-channel information. We will examine the limits of resolution polarization vision in stomatopods, using new methods.

Question 1. What is the sensitivity of polarization vision systems? Using new behavioural techniques, stomatopod and other invertebrate polarisation sensitivities will be described.

In 2012-13 we determined that stomatopods have surprisingly coarse spectral and polarisation resolution, using this new behavioural technique. Conversely polarisation resolution in cuttlefish and fiddler crabs is fine. As with colour processing (Fig. 2) this indicates a new form of information processing.

In 2014 we will develop models and circuit-diagrams that account for this difference between stomatopods and other animals, test other stomatopod species and other non-stomatopod species for polarisation resolution.

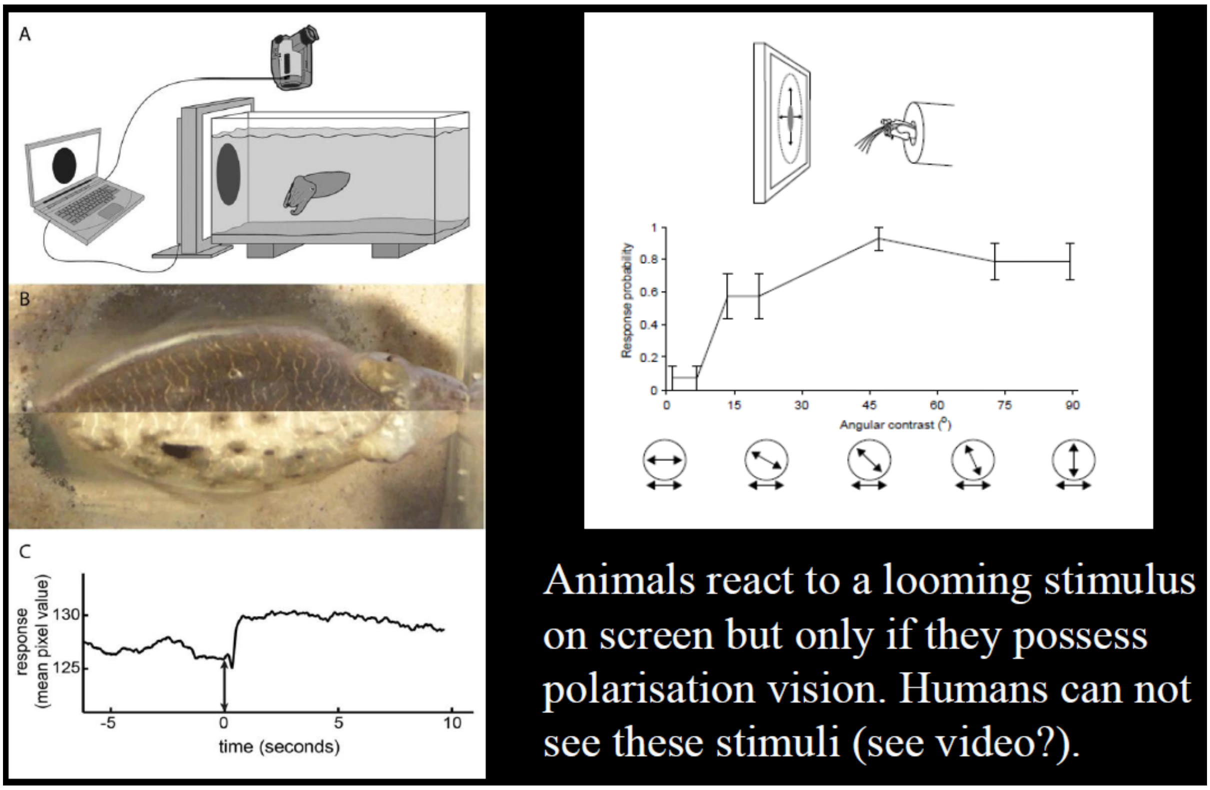


Figure 1 Polarisation test paradigm A-C Left, show setup with cuttlefish. The looming black circle can only be seen by animals with polarisation vision and their reaction is recorded. Cuttlefish blanch or change body colour as shown in B – top half before, bottom half after stimulus. This can be quantified using pixel brightness and is sensitive down to one degree of polarisation difference. Stomatopods (Right) also react to similar looming stonuli by retreating or showing eye movements. However, the reaction threshold is far coarser than expected and is closer to 15 degrees.

Question 2. How are stomatopod-type line scan systems optimized for multi-channel acquisition and information processing?

Using tests for colour vision (and with manuscript currently submitted to Science), we have shown conclusively that stomatopods process information in parallel and without comparison between input channels. This is a completely new way to analyse information and means the stomatopod system may operate to examine surfaces as a full spectrum ellipsometer might build information to populate a matrix.

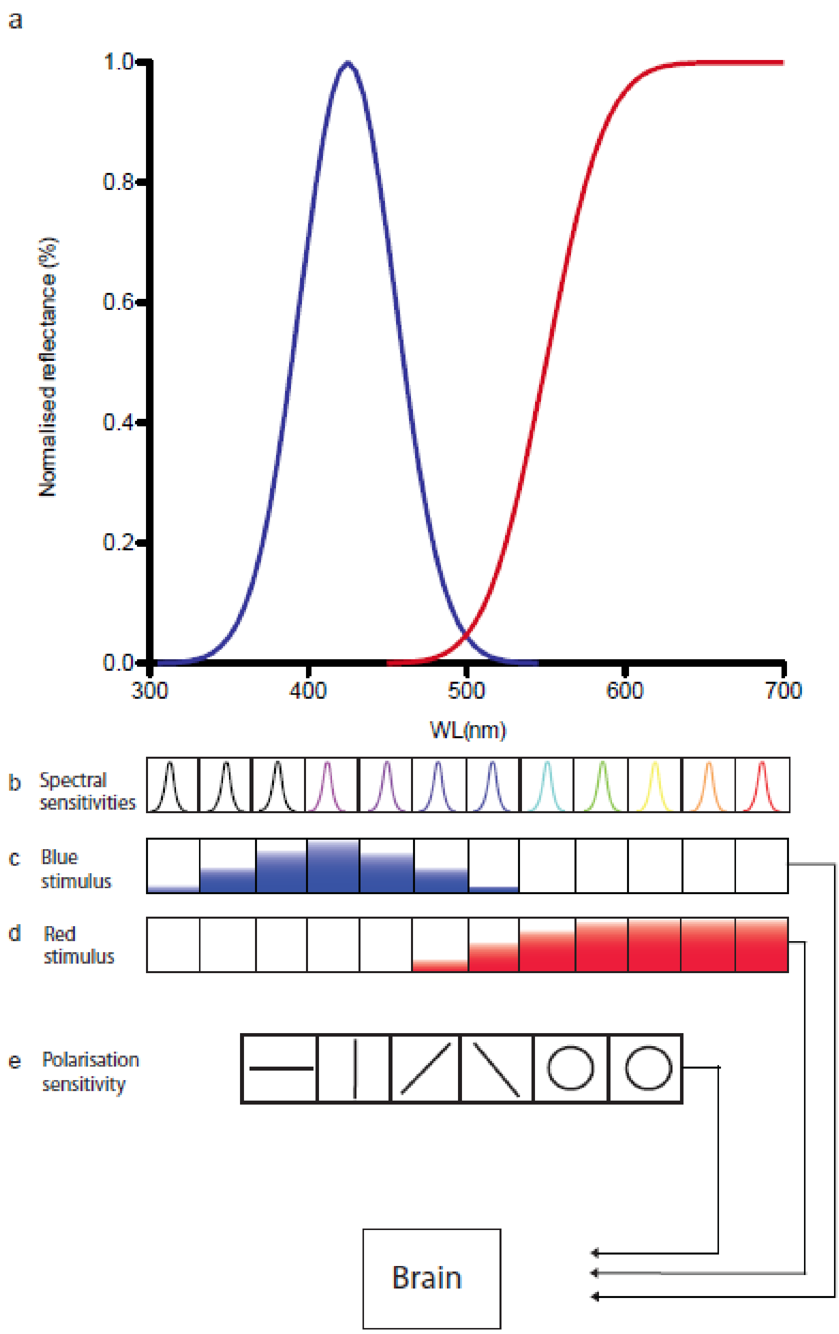


Figure 2 Proposed processing mechanism. a) Idealised spectral reflectance from stomatopod body parts b) Spectral sensitivities throughout the spectrum divided into separate bins. c) and d) Excitation patterns of each spectral sensitivity when looking at the blue c) and the red d) reflectance spectra. e) Polarisation system in stomatopods with, respectively, linear (90° angles), elliptical (45° angles) and circular (circles) polarisation sensitivities binned in the same way as the spectral sensitivities.

Question 3.

Do animals with polarization sensitivity see further in scattering media? This is one of the experiments to be conducted in collaboration with the Roberts lab in June this year.

Preliminary results from these experiments, conducted in the field on The Great Barrier Reef, over two field trips suggest that PS can aid visual distance in turbid media in fish.

In 2013 this successful experimental protocol was transferred to stomatopods and will continue in 2014 with the addition of a new PhD student to the Roberts laboratory.

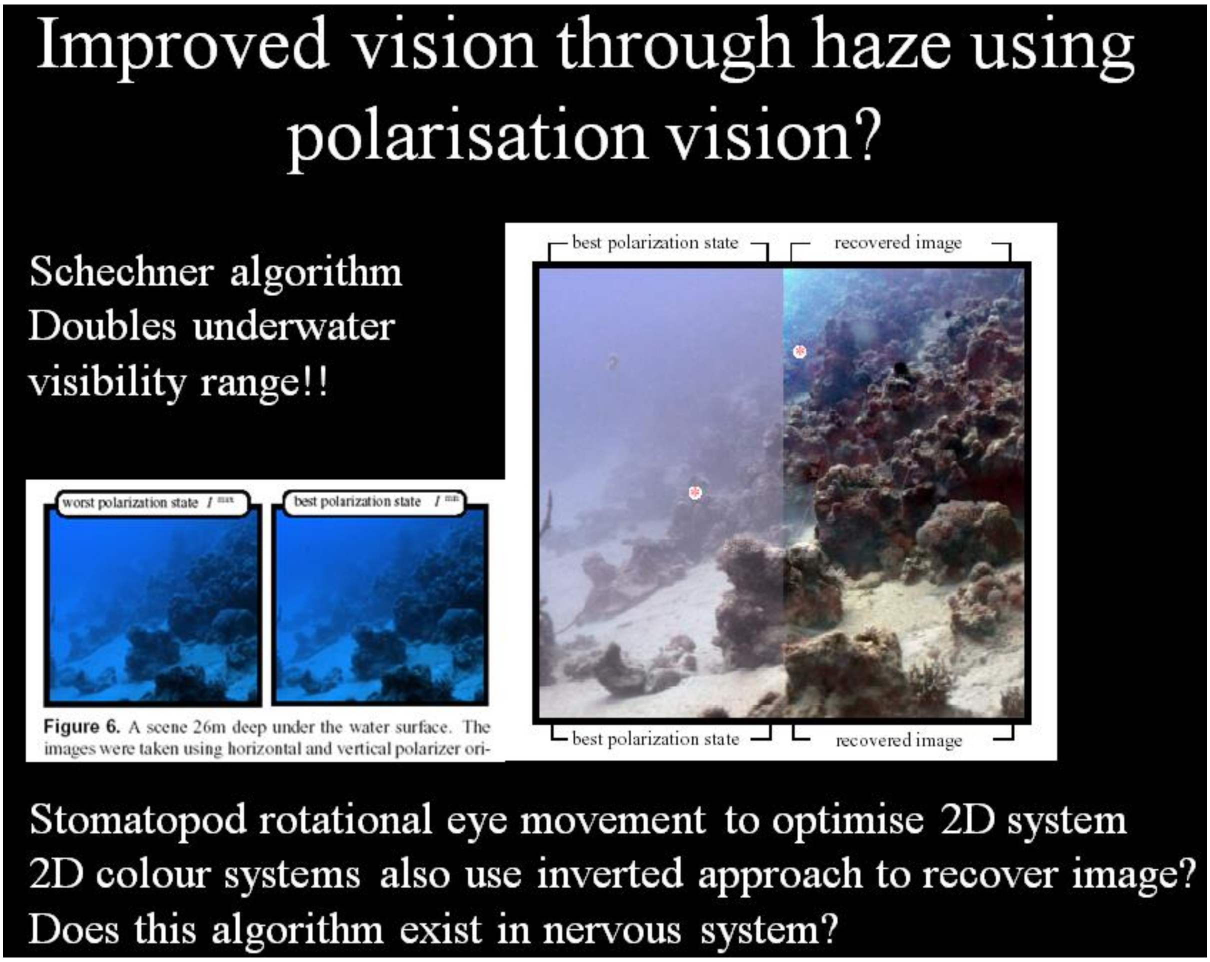


Figure 3 Greater visual penetration through de-hazing. In 2003 Yoav Schechner and colleagues combined machine vision principles and some inspiration from stomatopod vision to hypothesise that animals or sensor systems with only two channels of optimised linear polarisation could remove intervening polarisation scatter. The result is an improvement of underwater visual range of up to 50%. We are now testing this prediction with both stomatopod and fish models.

(2) To discover how information is processed in stomatopod visual systems. At higher levels, we will examine neural interconnectivity and processing principles at various stages of analysis in the visual system both anatomically and with electrophysiological approaches.

Question 1. How do the photoreceptor cells of mantis shrimps produce responses that track extremely transient changes in stimulus intensity?

Extracellular recordings of stomatopod visual responses are now complete and will tell us that stomatopods have a relatively rapid response time compared to other animals. Given the rapid behaviours they engage in, including ballistic strikes and fighting behaviour, this is expected.

In 2014 we will attempt to calculate if this visual rapidity is a result of the coarse nature or low bit-rate of the system.

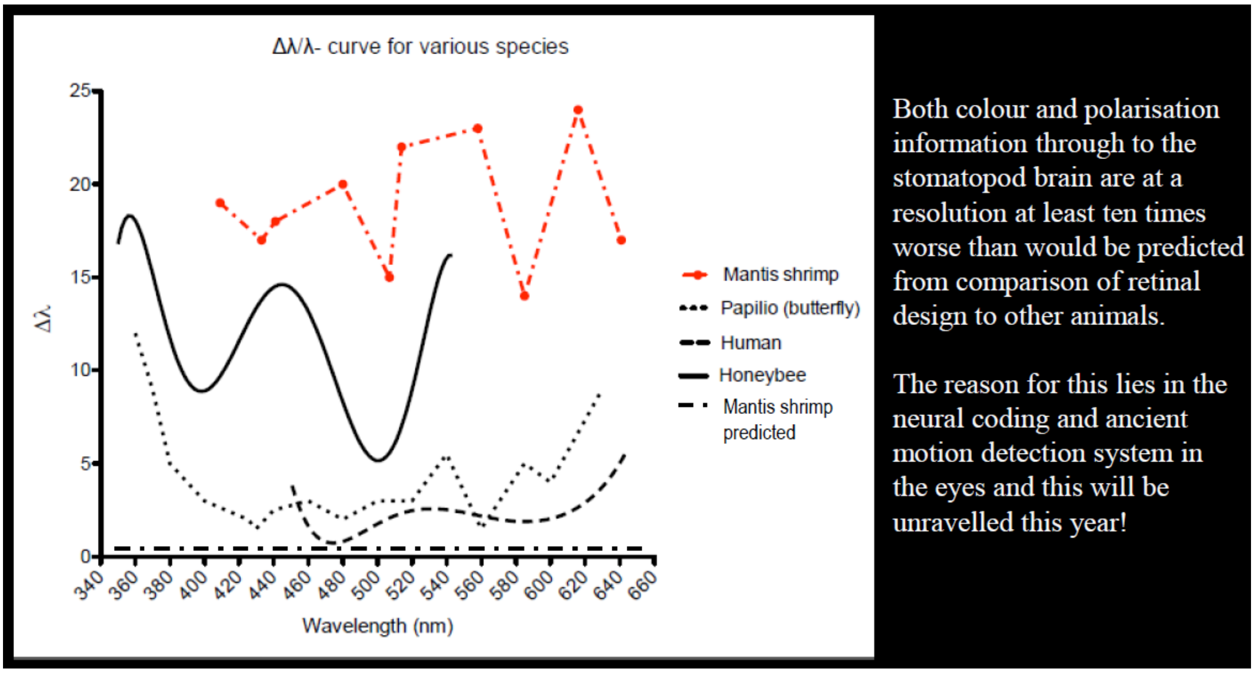


Figure 3 Spectral discrimination curves (Δλ/λ). Spectral discrimination curve from behavioural testing of *H. trispinosa* in thick black line, modelled spectral discrimination curve in thick dashed line. Figure modified from previous work on different animals as comparison. This indicates a low bit-rate for the stomatopod system.

Question 2. How are the neural circuits constructed to provide the information processing? This is a large question but will be started in 2013 along with the new PhD studentship and PostDoc for the project.

PhD student Hanne Thoen and New PhD student to the project Rachel Templin have begun high resolution transmission electrom microscopy and fluorescent staining of the stomatopod nervous system to determine information pathways arising from the various visual modalities. This will continue through 2013.

Question 3. What messages reach the stomatopod brain in a way that allows rapid decision making?

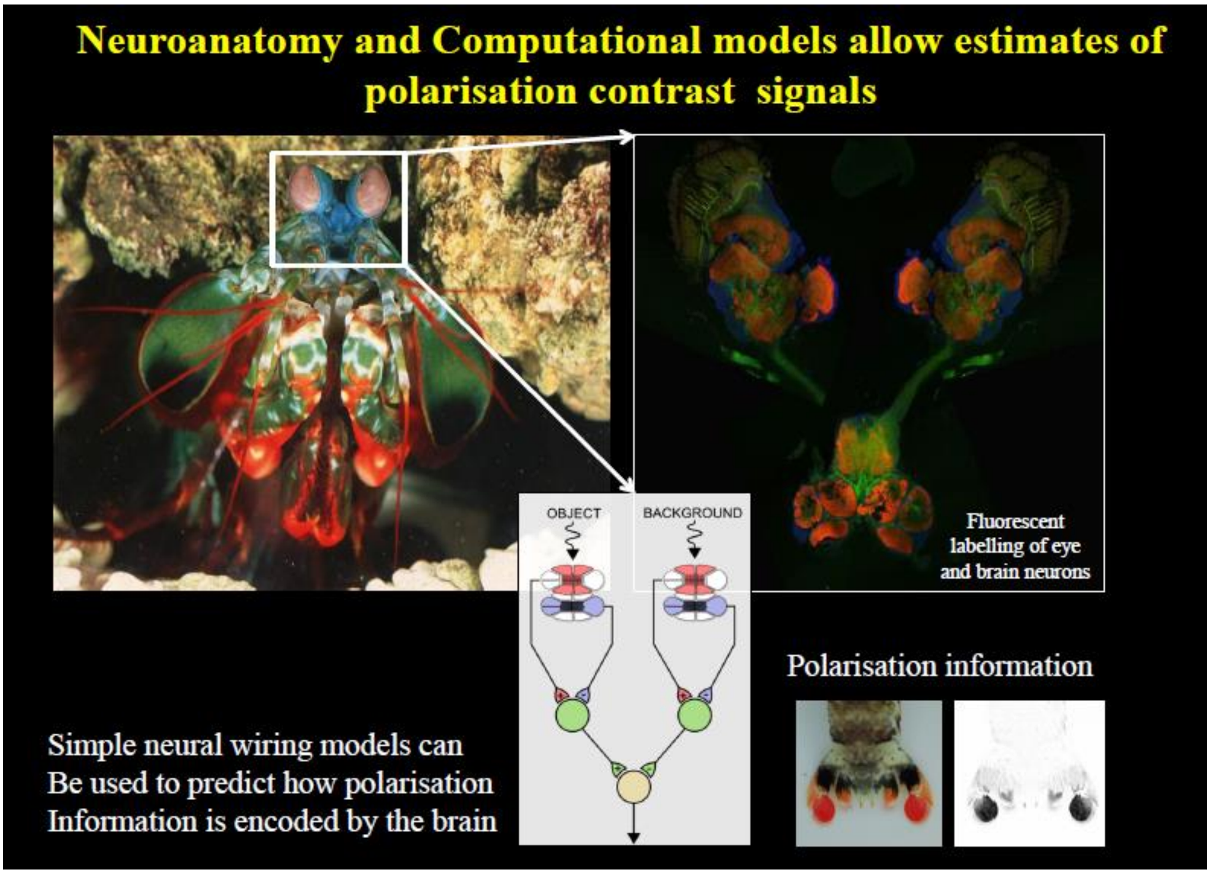


Figure 4 Neural connectivity and modelled polarisation discrimination system. Fluorescent labelling of stomatopod brain structures are revealing the information flow to the central processor. This enables models of the discrimination system to be developed where the polarisation difference between object and background is estimated.

(3) To discover the natural complexity of visual scenes the stomatopod imaging system has evolved to see. It is fundamental that we understand the visual information stomatopods see.

Question, development 1. Building a real-time Schechner-algorithm camera for visual enhancement underwater. Development of real-time polarisation cameras with collaborator Gruev is underway and we expect to trial V2 systems in June on The Great Barrier Reef.

In 2012 and 2013 V2 cameras were tested with great success on the GBR. This camera is in final stages of housing manufacture and will be 'released to the biologisys' in October this year.

2014, Circular polarising cameras will be developed and tested.

Question, development 2. Camouflage and communication underwater using polarized light. Imaging of animals in their natural habitat is continuing and should be almost completed in this year.

Silvery camouflage was examined in 2012 with a Nature publication resulting from this work. In 2013, further camouflage and communication in polarisation space were examined in both underwater and terrestrial habitats. Field observations support the idea that silvery fish do not camouflage well against polarising backgrounds and are easy prey to eg cephalopod predators.

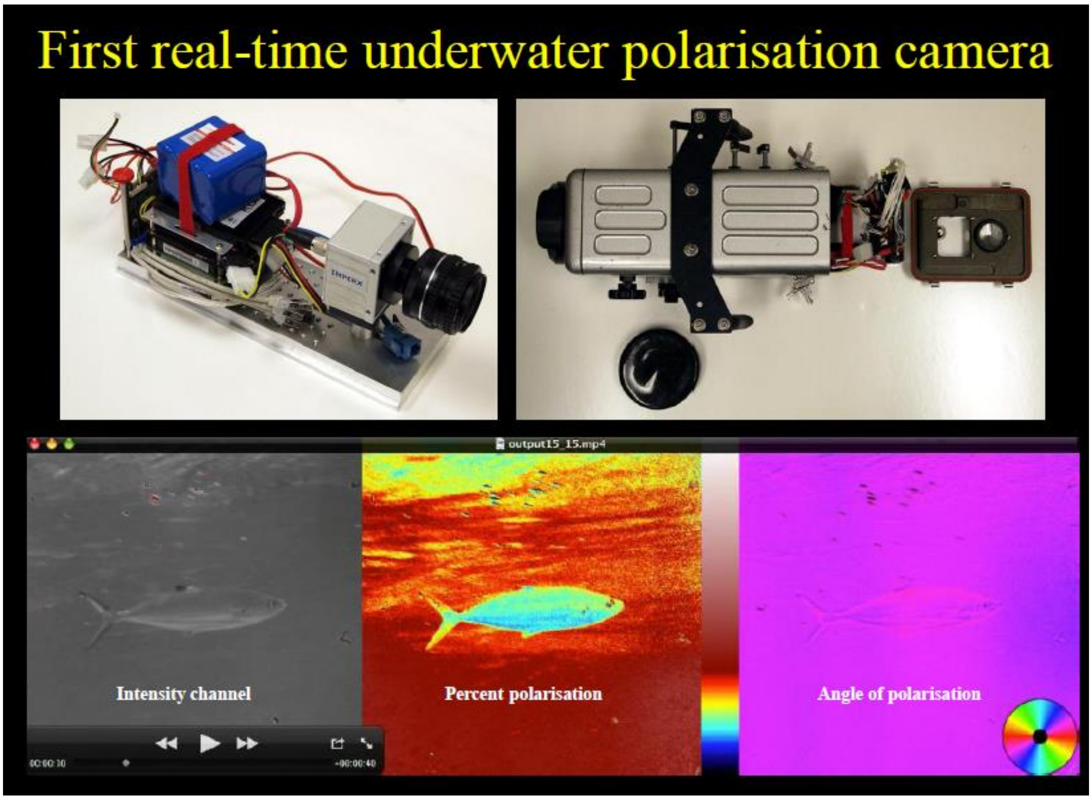


Figure 5 Camera design and real-time video frame results. Silvery fish are relatively well camouflaged in intensity and angle but are conspicuous in degree.

Question, development 3. Combined linear and circular polarization cameras. This is underway with Gruev lab.

A series of bio-inspired polarisation cameras with different functions and application is planned for the remaining years of the project

Question, development 4. Enhanced optical storage and information efficiency?

This is a year 3,4 question, once we know more about the pathways to the brain and the information content.

Question, development 5. A new generation of color-polarisation cameras with stacked rather than adjacent color channels. Another ‘technology’ already employed by stomatopods.

A year 3.4 question also.

(4) To investigate the co-evolution of visual systems, visual signals and camouflage in the natural environment. We will proceed from the above discoveries to relate how stomatopods see and what they see to our observations that species vary in the types of signals they produce.

Question 1. Are the polarization signals from different stomatopod species matched to species-specific elliptical polarization vision capability? New anatomical studies will be initiated this year to examine this question.

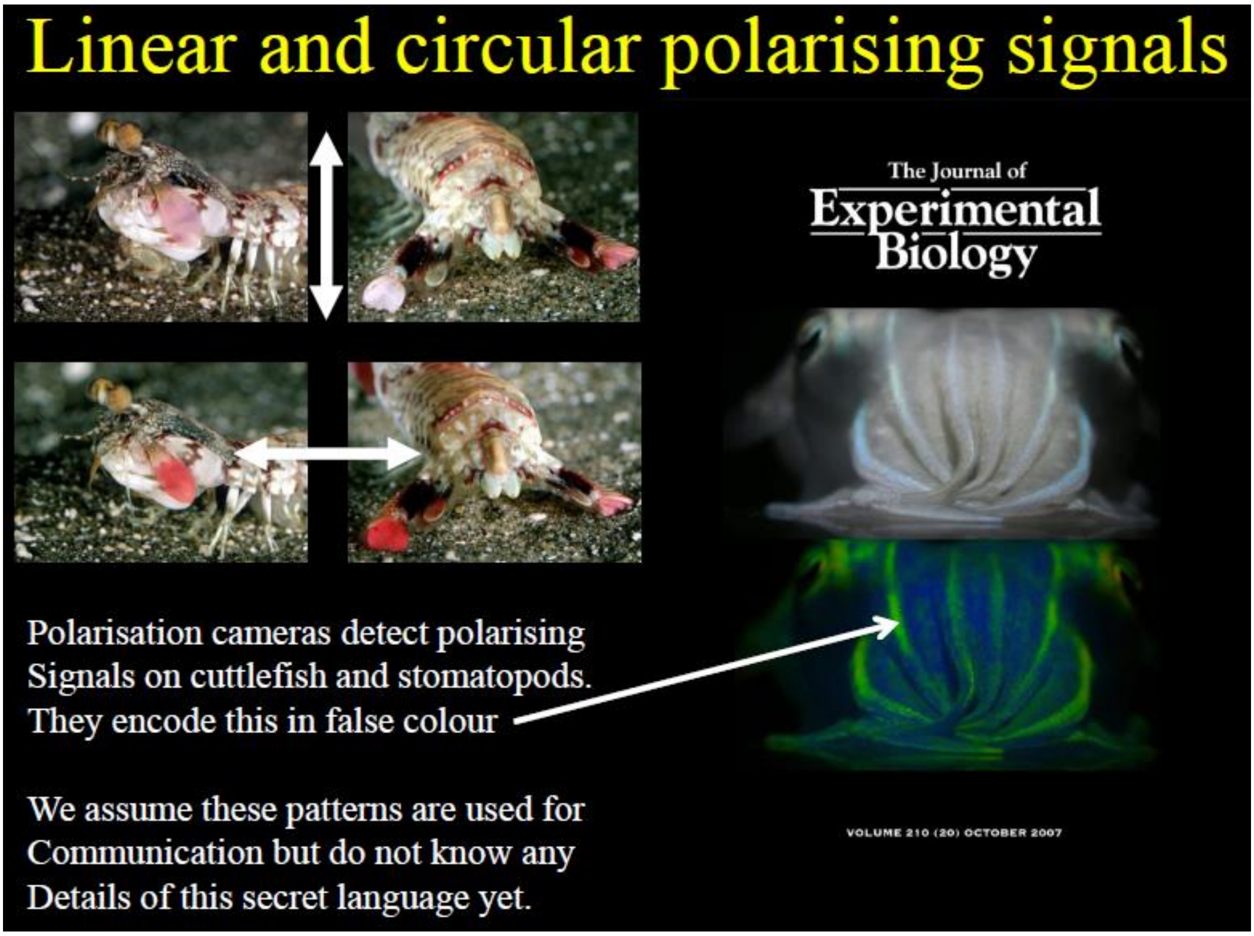


Figure 6 Polarisation signals. Stomatopods and cephalopods both produce polarising signals. The photonic method of production of these signals is under investigation with new results expected in 2014.

Question 2. As well as between species R8 differences (and therefore elliptical information tuning), very recent results suggest within-species differences in some species (Figs. 8&9). Is this the outcome of an ‘arms race’ in which there are generalist species, able to interpret the messages of prey, break prey camouflage, and ‘read the mail’ of the unsuspecting messengers?

In 2014 new ultra-high resolution electron microscopy will be used to optically model the retardation properties of different R8 cells. Use of this system was delayed in 2013.

Students and Marshall lab. personnel

The personnel involved in and supported by this project are summarized below:

Justin Marshall	PI
Martin How	PostDoc, salary supported
Yakir Gagnon	PostDoc, salary supported
Yi-Hsin Li	PostDoc, research supported 50%
Shelby Temple	PostDoc, research supported
Hanne Thoen	PhD, salary supported 50% (started April 2011)
Wen-Sung Chung	PhD, research supported
Rachel Templin	PhD, research supported

Where possible, we have sought to build the capacity of the grant through awards for students, travel and personnel costs. Example from the above list include PhD awards from Norway, Australia and Taiwan.

Publications in 2012-13

SE Temple, V Pignatelli, T Cook, MJ How, T-H Chiou, NW Roberts and NJ Marshall 2012. High Resolution polarisation vision in a cuttlefish. Curr. Biol. 22:R121.

NJ Marshall, KL Cheney. 2012 Vision and body colouration in marine invertebrates. In: The Visual Neurosciences eds Chalupa et al. MIT.

M.J. How, Pignatelli, V., Temple, S.E., Marshall, N.J. and Hemmi, J.M. 2012 High e-vector acuity in the polarisation vision system of the fiddler crab *Uca vomeris*. Journal of Experimental Biology. 215:2128-34.

N.W. Roberts, N.J. Marshall, and T.W. Cronin. 2012. High levels of reflectivity and pointillist structural color in fish, cephalopods, and beetles (letter). Proceedings of the National Academy of Sciences of the USA 109:E3387.

M.L. Porter, J.R. Blasic, M.J. Bok, E.G. Cameron, T.Pringle, T.W. Cronin, and P.R. Robinson. 2012. Shedding new light on opsin evolution. Proceedings of the Royal Society of London B 279:3-14.

RT Hanlon, C-C Chiao, L Mathger and NJ Marshall (In Press 2013) A fish-eye view of cuttlefish camouflage using in situ spectrometry. Biological Journal of the Linnean Society.

TW Cronin, S Johnsen, NJ Marshall and EJ Warrant (In Press 2013) Visual Ecology. Princeton University Press.

NJ Marshall and TW Cronin (In Press 2013) Crustacean Polarisation Vision. In: Polarisation Vision. G Horvath (ed). Springer, New-York.

NJ Marshall, TW Cronin and NW Roberts (In Press 2013) Polarisation Signalling. In: Polarisation Vision. G Horvath (ed). Springer, New-York.

M.L. Porter, D.I. Speiser, S. Zaharoff, R.L. Caldwell, T.W. Cronin, and T.H. Oakley. (In Press 2013) The evolution of complexity of in visual systems of stomatopods: insights from transcriptomics. Integrative and Comparative Biology.

Three papers are currently submitted to Science, Current Biology and The Journal of Experimental biology on stomatopod vision and signal processing, cephalopod vision and range-finding optics and polarisation distance modelling respectively

Talks in 2012-13

M How, NJ Marshall 2012 Polarisation vision, an unexplored channel for communication? VDU 2012.

NJ Marshall AMSA-NZMSS 2012 Sensory biology in the Coral Sea and neighbouring waters. Hobart. (PLENARY)

M How and NJ Marshall 2012 “Modelling sensitivity to polarised light” Tenth International Congress of Neuroethology

S Temple, NJ Marshall et al 2012 “High-resolution polarization vision in cephalopods” Tenth International Congress of Neuroethology

H Thoen, M How and NJ Marshall 2012 “Understanding the complex visual system of Mantis Shrimps (Stomatopods); a new form of colour processingTenth International Congress of Neuroethology.

M Porter, M Bok, NJ Marshall TW Cronin 2012 “The evolution of polarization vision in stomatopods: molecules, signaling, and behavior” Tenth International Congress of Neuroethology”.

M How, NJ Marshall 2013 "Discrimination of objects in polarised light" International Conference on Invertebrate Vision.

Y-S Lee, CC Chou, NJ Marshall 2013 "Particle-mediated gene transfer as a new tool to examine cephalopod brain" International Conference on Invertebrate Vision.

NJ Marshall, TW Cronin, M How, H Thoen, S. Temple, N Roberts 2013. "Polarisationish, speaking the language and making the movie" International Conference on Invertebrate Vision.

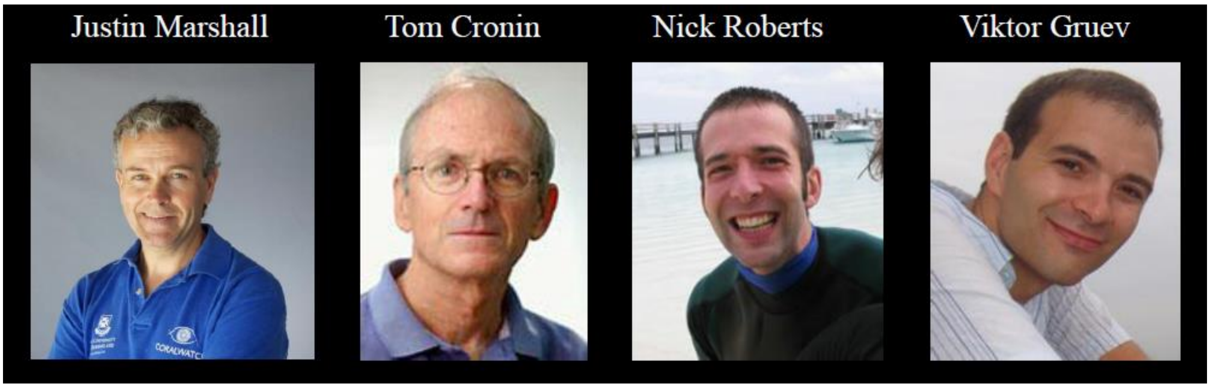
W-S Chung, NJ Marshall 2013 "A new form of range-finding using retinal deformation and image blurr in squid. International Conference on Invertebrate Vision.

H Thoen, M How, NJ Marshall 2013 "A new form of colour vision in mantis shrimp?" International Conference on Invertebrate Vision.

S Temple, N Roberts, NJ Marshall 2013 "Varying degrees of polarization vision in octopus: interaction between degree and angle of polarization in contrast detection tasks" International Conference on Invertebrate Vision.

Research Team Structure

The research program brings together laboratories in three different countries, Cronin (USA), Marshall (Australia), Roberts (Bristol, UK) and Viktor Gruev (Missouri, USA).



Almost all of the questions to be examined above are collaborative with this team and I have indicated this where possible so far. To summarise this, we expect milestones to be achieved in the following approximate proportions:

1) Efficiency and optimization in behaviour and task-solving.

Roberts	34%
Marshall	33%
Cronin	33%

2) Information processing, from molecular to behavioural levels.

Cronin	35%
Marshall	35%
Roberts	20%
Gruev	10%

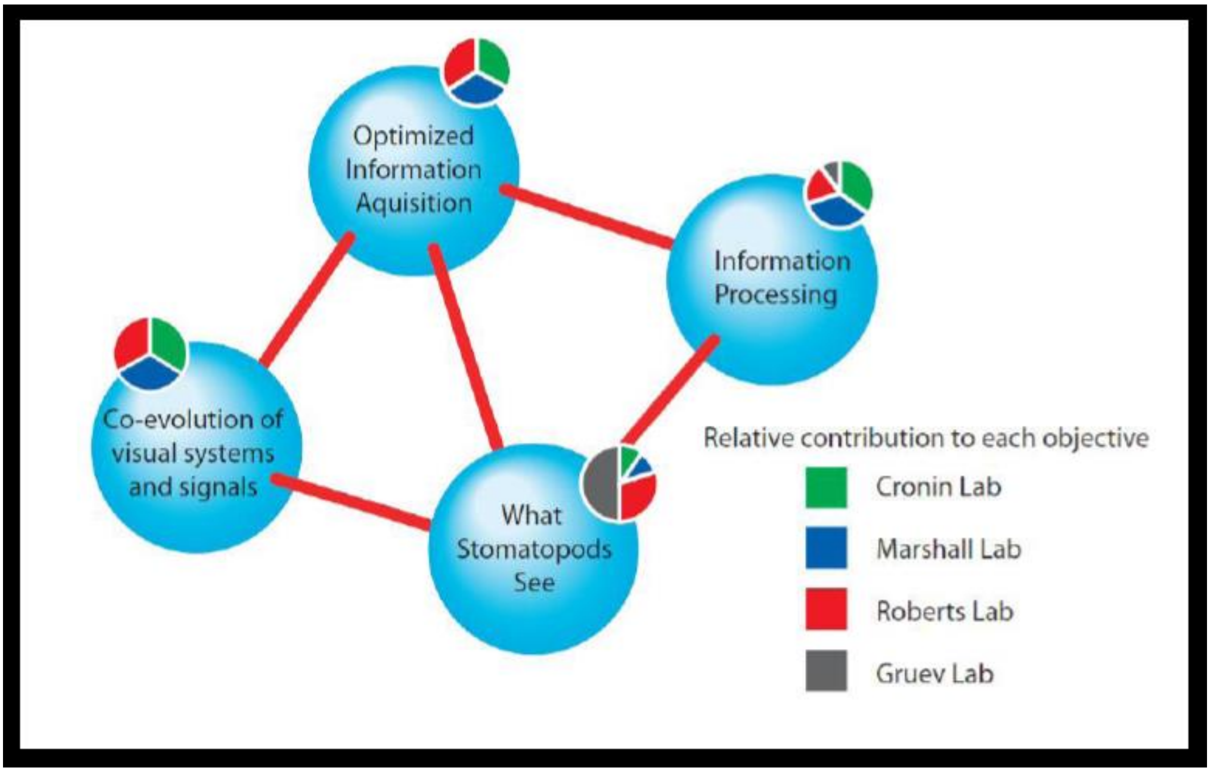
3) Testing biological principles through novel bio-inspired camera design.

Gruev	50%
Roberts	30%
Marshall	10%
Cronin	10%

4) The co-evolution of seeing and signals for optimal efficacy.

Marshall	34%
Cronin	33%
Roberts	33%

The diagram on the following page indicates the relative interactions of the four groups:


Optimized Information Aquisition
Information Processing
Co-evolution of visual systems and signals
What Stomatopods See
Relative contribution to each objective
Cronin Lab
Marshall Lab
Roberts Lab
Gruev Lab